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INFRAGENERIC CLASSIFICATION OF *RHEXIA* (MELASTOMATACEAE)

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ABSTRACT

An infrageneric classification of *Rhexia* is presented, based primarily on morphology. The 13 species are divided into four sections: (1) Sect. *RHEXIA* (*R. virginica*, the type; 9 species, divided informally into two morphological groups based on stem morphology); (2) **Sect. CYMBORHEXIA** Nesom, sect. nov. (*R. alifanus*, the type; 1 species); (3) **Sect. BREVIANTHERA** Nesom, sect. nov. (*R. petiolata*, the type; 2 species); and (4) **Sect. LUTEORHEXIA** Nesom, sect. nov. (*R. lutea* the type; 1 species). A diagnostic key to the sections and groups and comments on species delimitations in the *R. mariana* group are provided.

Rhexia comprises 13 species (see comments below), all of which are restricted to central and eastern North America (the USA and Canada) except for *R. cubensis*, which also occurs in the West Indies (Cuba, Hispaniola, Puerto Rico). The genus has been the subject of taxonomic studies (James 1956; Kral & Bostick 1969, largely repeating the James study, with addition of a new species and cytological data; Snyder 1996, a regional study) as well as a phylogenetic study (Ionta et al. 2007).

Rhexia has sometimes been treated as the monotypic tribe Rhexieae DC. The genus was hypothesized by Renner (1993) to be sister to tribe Merianieae Triana, but a later study (Clausing & Renner 2001) indicated that *Rhexia* is sister to *Arthrostemma* Pavón ex D. Don, a genus comprising seven species of herbaceous perennials native from Mexico and the West Indies to Bolivia in South America. The analysis by Fritsch et al. (2004) placed *Rhexia* and *Arthrostemma* as sister to the primarily Brazilian tribe Microlicieae, but wider sampling (Michelangeli et al. submitted) indicates that a clade that includes these two genera along with *Pachyloma* DC. (ca. 6 species, northern South America) is nested cladistically within the broader group that constitutes tribe Melastomeae.

The present account provides a formal infrageneric classification of *Rhexia*. It arose out of an attempt to understand the patterns of variation within the genus during preparation of a taxonomic treatment for the Flora of North America North of Mexico and the need for a summary of discussions and analyses by previous authors.

Species delimitations

Species of *Rhexia* recognized here and in the FNA treatment are similar to those of Kral and Bostick (1969) except in one instance. In the concept of Kral and Bostick, *R. mariana* includes the two tetraploid entities var. *ventricosa* and var. *interior* — the geographic ranges of both of the latter lie almost completely within that of the typical expression, which is diploid. Var. *mariana* is completely reproductively isolated from the tetraploid varieties, which form sterile seeds in experimental crosses. Variety *interior* and var. *ventricosa* are morphologically similar to each other but completely allopatric and each differs from var. *mariana* in a prominent feature of stem morphology — typical *R. mariana* has unequal stem faces (see below) while each of the two tetraploids has equal faces. Following James (1956), these two non-typical taxa are recognized here and at specific rank, apart from *R. mariana* in the strict sense. The morphological differences that separate these three entities are consistent and the ploidal differences contribute to the reproductive isolation that has been experimentally documented.

The biological situation is different in *Rhexia cubensis* (diploid, tetraploid, hexaploid), *R. nashii* (tetraploid, hexaploid), and *R. virginica* (diploid, tetraploid), where conspecific plants of different ploidy apparently occur sympatrically and are completely reproductively isolated (no seeds formed in experimental crosses), but there are no obvious morphological differences among them (see chromosome counts, geography, and crossing data in Kral and Bostick).

Rhexia mariana var. *exalbida* was formally recognized by James (1956) as distinct in its white flowers and linear leaves and, as mapped (his Fig. 15), centered mostly from southern Mississippi to Florida and north along the coastal plain to the Carolinas. James noted, however, that differences between var. *exalbida* and var. *mariana* are quantitative and intergrading. Kral and Bostick (1969) observed that recognition of var. *exalbida* "might be held tenable on the basis of the floras of the Atlantic and eastern Gulf coastal plains" but that intergradation with the typical expression, especially in the Florida panhandle across to outer coastal plain to Texas, suggested to them that only a single entity should be recognized. The geography of chromosome counts reported by Kral and Bostick indicates that both var. *mariana* and var. *exalbida* are diploid. Emphasizing its geographic concentration in the southeastern corner of the species range, var. *exalbida* is treated for FNA as distinct at varietal rank. Only the broader-leaved, purple-petaled plants (var. *mariana*) occur in the northern and western parts of the range; narrow-leaved, often white-petaled plants with small hypanthia appear to be nearly exclusive in peninsular Florida; intergrades are common in the narrower region between the extremes.

As noted by Kral and Bostick (1969), *Rhexia mariana* is the most abundant and wide-ranging of the species. It is sympatric with all other species and apparently hybridizes with several, the hybrids often seemingly taking on characteristics of the other species. Hybrids and hybrid swarms of *R. mariana* with *R. salicifolia*, *R. virginica*, and *R. nashii* have been observed (James 1956; Kral & Bostick 1969).

The taxonomy here of species and varieties in *Rhexia* exactly matches that of LeBlond (2010), who provides a useful pair of keys (one using all characters, the other using only vegetative features) to the species.

Infrageneric groups

Ideas about species groups in *Rhexia* have been discussed by earlier students of the genus (i.e., James 1956; Kral & Bostick 1969; Wurdack & Kral 1982; Ionta et al. 2007) and the groups formalized in the present account are for the most part similar to earlier ones.

Based primarily on anther morphology, James (1956) recognized two major groups among the species of *Rhexia*: "Series A," including *R. nuttallii*, *R. petiolata*, and *R. lutea*, and "Series B," including the rest of the species. Series B was noted to be "a very natural assemblage of species with the exception of *R. alifanus*" (emphasizing the anomalous seed morphology of the latter). He further divided Series A into two groups, observing that *R. lutea* differed in capsule morphology from the other two species, and Series B into subgroups, based first on stem morphology and then on root-rhizome morphology.

Kral and Bostick (1969) observed essentially the same pattern, for the most part closely following the discussion by James, adding that (p. 387) species of series A "show no tendency to cross-pollinate or at least do not produce successful hybrids, tend to have strikingly uniform morphologies over their range, and are less weedy. On the other hand most of the latter series [series B] (with the exception of *R. parviflora* and *R. alifanus*) do produce successful hybrids, show considerable diversity of morphology over their ranges, and are often weedy." They also noted (p. 388) that "On a basis of chromatographic and anatomical analysis of plant parts it would appear that

R. lutea in series 'A' and *R. alifanus* in series 'B' of James may actually represent distinct sections." The pattern observed by Wurdack and Kral (1982) was similar but they referred to four main groups ("four natural entities"), giving *R. alifanus* and *R. lutea* coordinate rank with series A and B.

Following Wurdack and Kral (1982), the present account recognizes four primary morphological groups (formal nomenclature validated below): (1) **sect. *Rhexia*** — series B of James excluding *R. alifanus*, (2) **sect. *Cymborhexia*** — *Rhexia alifanus* (3) **sect. *Brevianthera*** — series A of James excluding *R. lutea*, and (4) **sect. *Luteorhexia*** — *Rhexia lutea*. Each of the four sections appears to be monophyletic.

The species of sect. *Rhexia* are divided into two groups, corresponding to a difference in stem morphology. Data of Ionta et al. (2007, see comments below) suggest that the species of sect. *Rhexia* are likely to have reticulate relationships reflecting ancestral hybridization, thus the division into two groups may prove to be artificial. The apparent cauline specialization, however, is discontinuous and remarkably distinct.

Stems and roots

Inequality in width and morphology of stem faces has commonly been used in keys to species of *Rhexia* — one set of opposing faces is broader and convex, the other narrower, concave, and paler. Another correlated difference apparently has not been previously described or it has been noted only obliquely in descriptions. In those species with "unequal" faces, the nature of the faces abruptly alternates 90 degrees at each node. In a given plane, at each successive node a narrow-concave face abruptly becomes a broad-convex face and vice versa. This feature is unequivocally interpreted. In the Aequales group of sect. *Rhexia*, sect. *Brevianthera*, and sect. *Luteorhexia*, the four stem faces are similar in morphology ("equal") and continuous across the nodes from one internode to the next. Stem faces of *R. nuttallii* and *R. petiolata* (sect. *Brevianthera*) and *R. lutea* (sect. *Luteorhexia*) were scored as "unequal" by Ionta et al. (2007), in disagreement with the observation here, insofar as that term refers to the 'alternating' morphology. "Equal" stem faces also are characteristic of species of *Arthrostemma* (pers. observ. and as recorded by Ionta et al. 2007).

In *Rhexia alifanus*, stems are not clearly demarcated as four faces — instead they are terete proximally, with internodes distally somewhat flattened in a plane parallel to the subtending leaf pair and longitudinally striate, the narrower bands paler and aligned with the leaf midribs. Stems of *R. alifanus* were recorded as having "unequal" faces by Ionta et al., but the morphology is not similar to either the "equal" or "unequal" division into faces as in other species of the genus.

Vegetative reproduction in *sect. Rhexia* is through adventitious buds from long, laterally extending, lignescent, rhizome-like roots (Fig. 2). These structures were correctly identified as roots by James (1956), following the earlier, detailed study by Holm (1907), but their identification as rhizomes (or "stolons" or "rootstocks") has persisted (e.g., Kral & Bostick 1969; Godfrey & Wooten 1981; Ionta et al. 2007) without mention of the earlier-observed distinction between rhizomes and roots. Root tubers (tuberous swellings; Fig. 1) are produced in most species of sect. *Rhexia*. Plants of sect. *Brevianthera* and sect. *Cymborhexia* produce only short lignescent-fibrous roots without tubers.

In *sect. Rhexia*, the tuberous swellings may develop on the primary root at the very base of the stem or at irregular positions on secondary roots. Adventitious buds arise from tuberous and non-tuberous portions of the root.

Figure 1a, b. Vegetation reproduction in *Rhexia mariana* var. *mariana* through adventitious buds from rhizome-like roots. Root tubers are not produced in *R. mariana*. **Georgia**. Wayne Co.: NW of Sterling, 16 Aug 1993, *Kral 83069* (VDB).

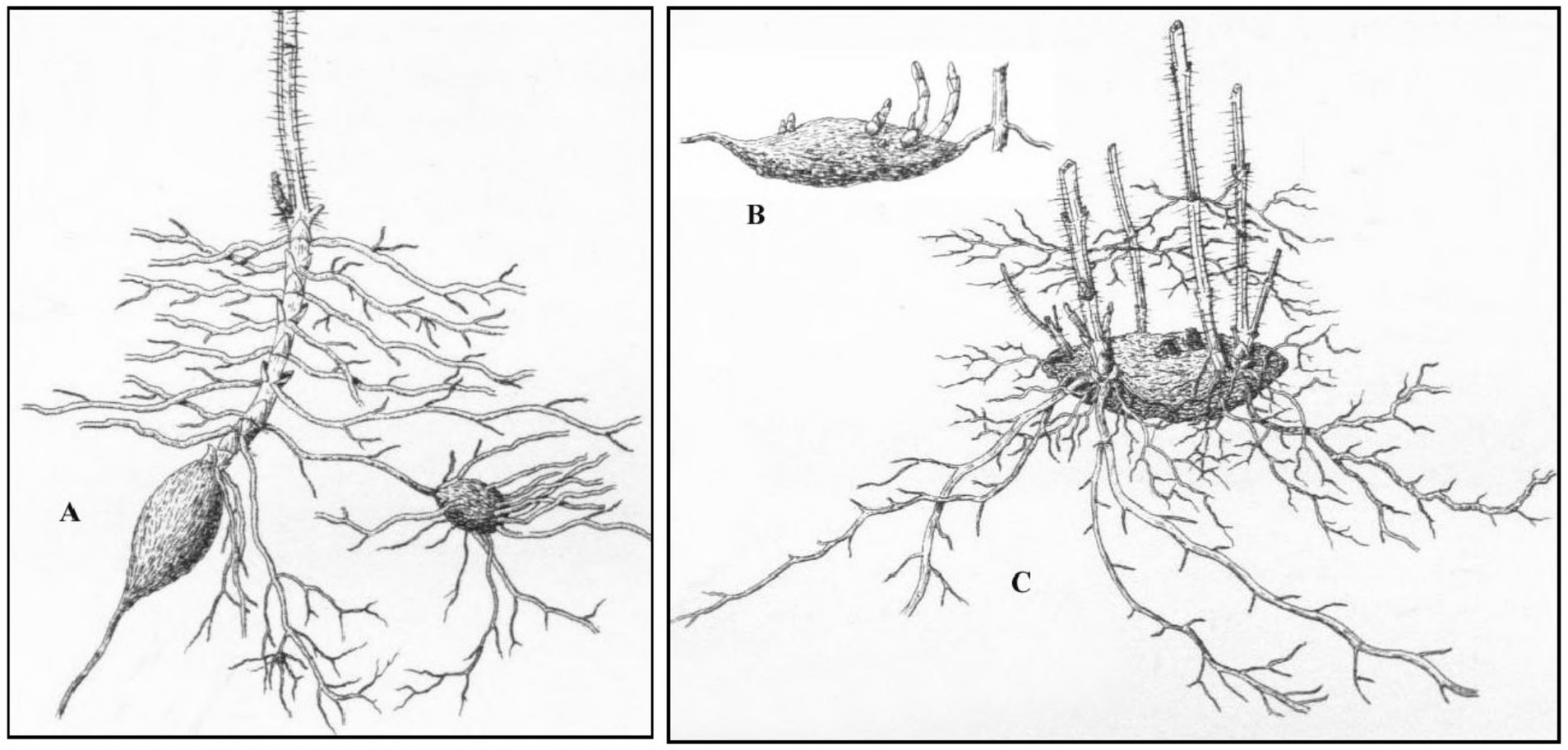

Figure 2a, b, c. Root tubers in *Rhexia virginica*, with adventitious buds and shoots originating from the tubers. From Holm (1907).

Phylogenetic study of Ionta et al.

Ionta et al. (2007) studied phylogenetic relationships among *Rhexia* species using DNA sequence data — ribosomal nuclear (ITS), chloroplast (trnC-D), and nuclear (ncpGS) — and a morphological data set of 37 characters, with outgroups (following Renner and Meyer 2001, Renner et al. 2001) as species of *Arthrostemma* and *Dissotis* Benth.

The ITS and trnC-D topologies "differed in the phylogenetic positions of several taxa (*Rhexia lutea*, *R. nashii*, and *R. salicifolia* [also of *R. cubensis*]), and for *R. cubensis*, *R. lutea*, *R. nashii*, *R. parviflora*, and *R. salicifolia*, we recovered multiple alleles of ncpGS, which is single copy in most species of *Rhexia*, indicating that these individuals may be of hybrid origin" (Ionta et al. 2007, p. 1055). Evidence suggests that *R. nashii* originated as a hybrid between the two groups of sect. *Rhexia* — one of its ncpGS alleles is sister to *R. mariana* while the other is sister to *R. virginica*.

Analyses of pruned data sets (eliminating taxa that appeared in different places in the ITS and trnC-D topologies and/or that had two copies of ncpGS) using all three molecular regions plus the morphology resulted in a single, strongly supported most parsimonious tree with three major clades: *Rhexia petiolata* (sect. *Brevianthera*), *R. mariana* (Inaequales group), and *R. virginica* (Aequales group).

Rhexia lutea shows as sister to the whole genus in the trnC-D analysis and as sister to the Inaequales group of sect. *Rhexia* in the ITS analysis. Morphology, in contrast, places it as sister to sect. *Brevianthera*. Advanced characters strongly linking these two groups (90% bootstrap value), as scored by Ionta et al., are glabrous petals (homoplasious), curved-ascending petals, strongly and shortly constricted hypanthia, and short anthers. As noted by Ionta et al. (p. 1065), this indicates that morphological synapomorphies of *R. lutea* with sect. *Brevianthera* "may be homoplasious ... or were passed to *R. lutea* as a result of ancient hybridization with a member (either extinct or extant) of the *R. petiolata* clade." Observation of multiple heterozygous ncpGS loci also supports this possibility.

Rhexia alifanus shows as sister to the Inaequales group of sect. *Rhexia* in the morphological analysis. Ionta et al. noted, however (p. 1061), that this position is not well supported. "Putative synapomorphies linking *R. alifanus* with this clade include leaf stomatal distribution ... and anthers

with elongated, narrowly conical-filiform dorsal connective appendages ... ." Equal distribution of stomates on both leaf surfaces occurs in *R. alifanus* and in *R. salicifolia* and *R. aristosa* (Aequales group) and *R. parviflora* and *R. cubensis* (Inaequales group), hardly supporting a link to one or the other group, if indeed the state is apomorphic. Conical anther appendages, which are present in *R. alifanus*, are present in *R. marilandica*, *R. nashii*, and *R. cubensis* (Inaequales group) but also in *R. virginica* (Aequales group).

Molecular data from all three genes, in contrast to the morphology, place *Rhexia alifanus* is sister to sect. *Brevianthera*. There appears to be no morphological character of *R. alifanus* that might be unequivocally interpreted as synapomorphic with sect. *Brevianthera*.

Infrageneric classification

RHEXIA L., Sp. Pl. 1: 346. 1753. **TYPE**: *Rhexia virginica* L.

1. **Sect. RHEXIA TYPE:** *Rhexia virginica* L.

Anthers elongate, (3–)4–8(–11) mm long, curved, opening by small pores, surfaces minutely papillate; caudex absent or weakly developed; roots long, laterally extending, budding adventitiously, with tuber-like swellings (in the interpretation here, this tendency lost in *R. parviflora* and in *R. mariana*, *R. interior*, and *R. ventricosa*); stems branched to unbranched or nearly so, axillary buds suppressed or not, stem faces subequal or unequal (see comments above, "Stems and roots"), hairy at least at nodes; leaves bifacial (dorsiventral), surfaces not glaucous; stomates mainly on abaxial lamina surface or more or less equally distributed on both surfaces; hypanthia with a short but distinctly tubular neck; petals plane and horizontal, petals white to pink to lavender or purple; capsule dehiscence only in the apical depression; seeds cochleate, 0.6–0.75 mm long, surfaces variously sculptured; chromosomes small (see comment under sect. *Cymborhexia*); diploids and polyploids.

1a. The Equales group

Species included: *R. aristosa* Britt. (2x), *R. salicifolia* Kral & Bostick (2x), *R. virginica* L. (2x, 4x), *R. interior* Pennell (4x), *R. ventricosa* Fern. & Griscom (4x)

Stem faces subequal; stomates on abaxial lamina surface (*R. virginica, R. interior*, *R. ventricosa*) or more or less equally distributed on both surfaces (*R. aristosa*, *R. salicifolia,*).

1b. The Inaequales group

Species included: *R. mariana* L. (2x), *R. cubensis* Griseb. (2x, 4x, 6x), *R. nashii* Small (4x, 6x), *R. parviflora* Chapm. (2x)

Stem faces unequal (see comments in text); stomates mainly on abaxial lamina surface (equally distributed on both surfaces in *R. cubensis*).

The anthers of *Rhexia parviflora* are relatively shorter (3–3.5 mm long) than those of other species of sect. *Rhexia*. James (1956) noted the difference in length but observed that the curvature, small pores, and papillate surfaces are similar to the anther morphology of his series B. The plane-horizontal petals also are similar to sect. *Rhexia* and the unequal stem faces suggest that its ancestry is connected with others of the Inaequales group, especially with *R. mariana*, which also produces white flowers.

Figure 3a, b, c, d. Representative species of the four sections. a. *Rhexia alifanus*. b. *Rhexia virginica*. c. *Rhexia petiolata*. d. *Rhexia lutea*. Photos a, b, and d by James Van Kley, from the Pineywoods Plants Digital Gallery; c by Fred Nation from the Alabama Plant Atlas website.

2. **Sect. CYMBORHEXIA** Nesom, sect. nov. **TYPE**: *Rhexia alifanus* Walt.
Species included: *R. alifanus* Walt. (2x)

Anthers 7–8 mm long, curved, opening by small pores, surfaces smooth; caudex distinct, woody; roots short, fibrous, without adventitious buds or tubers; stems unbranched or nearly so, axillary buds suppressed, stems faces not demarcated, without ridges, terete proximally, internodes distally somewhat flattened in a plane parallel to that of the subtending leaf pair, longitudinally striate, the narrower bands paler and aligned with the leaf midribs), completely glabrous; leaves isofacial, surfaces glaucous, stomates more or less equally distributed on both surfaces; hypanthia with a very short but tubular neck; petals plane and horizontal, lavender-rose; capsule dehiscence only in the apical depression; seeds oblong-cuneate, subprismatic, 1–2 mm long, surfaces nearly smooth; chromosomes large (Kral and Bostick 1969 noted that the chromosomes of *R. alifanus* are relatively large compared to those in all other species); diploid.

3. **Sect. BREVIANTHERA** Nesom, sect. nov. **TYPE**: *Rhexia petiolata* Walt.
Species included: *R. nuttallii* C.W. James (2x), *R. petiolata* Walt. (2x)

Anthers 1.2–2 mm long, straight, opening by large pores, surfaces smooth; caudex strongly (*R. lutea*) or weakly developed; roots short, fibrous, without adventitious buds or tubers; stems unbranched or nearly so, axillary buds suppressed, stem faces subequal, glabrous; leaves bifacial, surfaces not glaucous, stomates mainly on abaxial lamina surface; hypanthia with an indistinct neck region, abruptly constricted above the locules and then immediately flaring into the lobes; petals curved and ascending, lavender to purple or pink; capsule dehiscence by a partial separation of the capsular segments; seeds cochleate, 0.6–0.7 mm long, surfaces variously sculptured; chromosomes relatively small; diploids and polyploids.

4. **Sect. LUTEORHEXIA** Nesom, sect. nov. **TYPE**: Rhexia *lutea* Walt.
Species included: *R. lutea* Walt. (4x)

Anthers ca. 2 mm long, straight, opening by large pores, surfaces smooth; caudex strongly (*R. lutea*) or weakly developed; roots short, fibrous, without adventitious buds or tubers; stems conspicuously branched, axillary buds not suppressed, stem faces subequal, hairy; leaves bifacial, surfaces not glaucous, stomates mainly on abaxial lamina surface; hypanthia with an indistinct neck region, abruptly constricted above the locules and then immediately flaring into the lobes; petals curved and ascending, yellow; capsule dehiscence only in the apical depression; seeds cochleate, 0.6–0.7 mm long, surfaces variously sculptured; chromosomes relatively small; polyploid.

KEY TO SECTIONS AND GROUPS OF *RHEXIA*

1. Anthers 1.2–2 mm long, straight, surfaces smooth, opening by large pores; petals curved and ascending.

    2. Petals lavender to purple or pink; stems unbranched or nearly so, axillary buds suppressed, stem faces completely glabrous; inflorescences strongly condensed, obscured by foliaceous bracts; leaves short-petiolate ..... 3. sect. **BREVIANTHERA**
    2. Petals yellow; stems conspicuously branched, axillary buds not suppressed, stem faces hairy; inflorescences diffuse, bracteate but not obscured by bracts; leaves subsessile
    ..... 4. sect. **LUTEORHEXIA**

1. Anthers (3–)4–8(–11) mm long, curved, surfaces smooth or minutely papillate, opening by small pores; petals plane and horizontal.

3. Caudex distinct, woody; roots short, ligneous-fibrous, without tubers; leaves isofacial, surfaces glaucous; anther surfaces smooth; seeds oblong-cuneate, subprismatic, 1–2 mm long, surfaces smooth; chromosomes large ..... 2. sect. **CYMBORHEXIA**
3. Caudex absent or weakly developed; roots often long and rhizome-like, commonly tuberiferous; leaves bifacial (dorsiventral), surfaces not glaucous; anther surfaces minutely papillate; seeds cochleate, 0.6–0.75 mm long, surfaces variously sculptured; chromosomes small 1. sect. **RHEXIA**

4. Stem faces subequal ..... 1a. Aequales group
4. Stem faces unequal ..... 1b. Inaequales group

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